

THE GENERA OF BAMBUSOIDEAE (GRAMINEAE) IN
THE SOUTHEASTERN UNITED STATES^{1,2}GORDON C. TUCKER³Subfamily BAMBUSOIDEAE Ascherson & Graebner, *Synop. Mitteleurop. Fl.*
2: 769. 1902.

Perennial or annual herbs or woody plants of tropical or temperate forests and wetlands. Rhizomes present or lacking. Stems erect or decumbent (sometimes rooting at the lower nodes); nodes glabrous, pubescent, or puberulent. Leaves several to many, glabrous to sparsely pubescent (microhairs bicellular); leaf sheaths about as long as the blades, open for over 1/2 their length, glabrous; ligules wider than long, entire or fimbriate; blades petiolate or sessile, elliptic to linear, acute to acuminate, the primary veins parallel to—or forming an angle of 5–10° with—the midvein, transverse veinlets numerous, usually conspicuous, giving leaf surface a tessellate appearance; chlorenchyma not radiate (i.e., non-kranz; photosynthetic pathway C₃). Inflorescences terminal or terminal and lateral, paniculate, the primary branches nearly horizontal, scabrous and/or hispidulous throughout; secondary branches often (and tertiary branches sometimes) present. Spikelets oblong to lanceolate, subterete to strongly dor-

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²For an account of the family, its subfamilies, and tribes, see C. S. Campbell, The subfamilies and tribes of Gramineae (Poaceae) in the southeastern United States. *Jour. Arnold Arb.* **66:** 123–199. 1985.

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siventrally compressed, 1- to 3- or more flowered. Glumes 0-2, subequal to decidedly unequal, broadly lanceolate, shorter than the lemmas, sometimes aristate, nerveless or weakly 1- or 3-nerved, glabrous. Lemmas narrowly elliptic, aristate or not, margins inrolled around the flower, the abaxial surface glabrous, scabrous, hispid (especially apically), or sometimes densely covered with stiff, clavate to uncinata trichomes. Paleas narrowly elliptic to lanceolate, shorter than lemma (lacking in staminate spikelet). Flowers perfect or imperfect (if imperfect the plants monoecious). Lodicules 0-3 [-12 in *Ochlandra*]. Stamens [1] 2, 3, or 6; filaments filiform, shorter than the lemmas; anthers linear, the apices of the connectives not prolonged. Ovaries narrowly elliptic, glabrous; styles terete basally, stigmas 2 or 3, equaling or longer than the styles, plumose or glandular-stipitate. Fruit a caryopsis or an achene (see *Zizaniopsis* and *Luziola*) [or a berry], ovoid, ellipsoid, or narrowly oblong, often tightly clasped by the indurate lemma and palea. Pericarp adnate to the seed or not; hilum linear; embryo less than $\frac{1}{3}$ as long as the caryopsis. Germination epigeal. Base chromosome number 12. (Including *Oryzoideae* Parodi ex Caro, Dominguezia 4: 10. 1982.) TYPE GENUS: *Bambusa* Schreber.

The Bambusoideae consist of three large groups: the woody bambusoids, represented in our area by tribe Bambuseae Dumort. (including tribe Arundinarieae Ascherson & Graebner); the herbaceous bambusoids, represented by tribes Phareae Stapf and Brachyelytreae Ohwi; and the oryzoids, represented by the Oryzaceae Dumort.

Members of the Phareae are distinguished from all other New World grasses by their leaf blades with divergent, rather than parallel, lateral veins. Species of this tribe (and of the related tribe Streptogyneae C. E. Hubb. ex Calderón & Soderstrom, of the Old World) are the only grasses with resupinate leaf blades. In most bambusoids the greatest density of stomata is on the lower (abaxial) surface, but in the Phareae it is on the adaxial (physically lower) surface. The Phareae comprise three genera. *Scrotochloa* Judziewicz (two species) and *Leptaspis* R. Br. (three species) are widespread in the Old World Tropics. *Pharus* P. Br. (seven species) is widespread in the New World Tropics and is represented in the United States by *P. lappulaceus* Aublet in central and northern Florida. It differs from the other two genera of the tribe in having persistent staminate spikelets and carpellate glumes with the margins free.

The unigenic tribe Brachyelytreae has often been placed elsewhere than in the Bambusoideae. Bentham (1883) assigned *Brachyelytrum* to the Poöideae, while Honda put it in the Stipeae. Reeder (1957) showed that its embryo was bambusoid, and MacFarlane & Watson showed that it did not belong in the Poöideae. Recently, Campbell and colleagues have summarized previous work and added new data that clearly demonstrate its bambusoid affinities. Similarities shared with the woody and herbaceous bambusoids include stomata on the abaxial leaf surface only (Renvoize) and cross veins in the leaves. Within the Bambusoideae, *Brachyelytrum* is clearly most closely related to the herbaceous bambusoids, but the genus is sufficiently different to warrant its own tribe.

The Bambuseae are the only free-standing, woody-stemmed grasses in North

America.⁴ The tribe comprises three (or four) subtribes (Bentham, 1883; Dahlgren *et al.*; Hackel, 1887; Hubbard). It is represented in the Southeast by only two native species of *Arundinaria* (subtribe Arundinariinae Bentham). Subtribes Bambusinae Hackel and Dendrocalaminae Bentham are each represented by one or more cultivated species that persist after cultivation. However, none of these nonnative species is known either to reproduce sexually or to establish new populations by seed, so they are not considered to be naturalized (Soderstrom, pers. comm.).

Plants of the Arundinariinae are generally smaller (usually less than 10 m tall) than other woody bamboos. The flowers have three stamens, and the fruit is a caryopsis. About six genera occur in both the Old World and the New. *Arundinaria* Michx. (ca. 100 species) has two species in the Southeast, *A. gigantea* (Walter) Muhl. and *A. tecta* (Walter) Muhl., and these are the only representatives of this genus indigenous in the New World. Two closely related genera occur in the Neotropics: *Arthrostylidium* Rupr., of the lowlands, and *Chusquea* Kunth (including *Retzbergia* Raddi), of the mountains. In eastern Asia the subtribe is represented by species of *Sasa* Makino & Shibata, *Pleioblastus* Nakai, *Semiarundinaria* Makino, and *Pseudosasa* Nakai. Some of these genera were originally included in *Arundinaria*; their segregation from that genus is by no means generally agreed upon.

Pseudosasa japonica (Sieb. & Zucc.) Makino is cultivated in the eastern United States. It sometimes escapes from cultivation and spreads by rhizomes (specimens seen from central New Jersey, eastern Pennsylvania, eastern Maryland, North and South Carolina, and central Florida). It can be distinguished from other native and nonnative bamboos in the Southeast by its persistent stem-leaf sheaths, glaucous lower internodes, and branches solitary at each node.

Certain genera of the subtribe that have deltoid glumes have been segregated as subtribe Phyllostachyinae Hackel. The genus *Phyllostachys* Sieb. & Zucc., native to China, includes about 80 species. At least 20 species are cultivated in the warmer regions of the United States (McClure, 1957), and at least one of these is hardy as far north as Boston, Massachusetts (C. E. Wood, Jr., pers. comm.). *Phyllostachys aurea* A. & C. Riv., golden bamboo, and *P. Meyer* McClure have been collected as possible escapes in North and South Carolina, Georgia, and Florida.

Plants of subtribe Bambusinae are tall; several species reach 30 m in height. The flowers generally have six stamens, and the fruit is a caryopsis. The largest genus, *Bambusa*, has about 70 species, all restricted to the Old World. Its New World counterpart, *Guadua* Kunth, with about 30 species, is distinguished by the winged keel of its paleas. McClure (1973), who believed that this difference was not consistent, treated the group as *Bambusa* subg. *Guadua* (Kunth) Hackel. Several species of *Bambusa* are cultivated in the Southeast and on the west

⁴The members of the Neotropical genus *Lasiacis* Hitchc. (subfam. Panicoideae A. Braun), represented by two species in Florida, are indurate to woody-stemmed, weakly clambering plants with subterete spikelets. Southeastern bamboos (both native and nonnative) are free-standing plants bearing dorsiventrally flattened spikelets.

coast from California at least as far north as Portland, Oregon. Individual clones may persist for many years after cultivation. *Bambusa vulgaris* Schrader sometimes continues to grow around old house sites in southern Florida (Long & Lakela). *Bambusa multiplex* (Lour.) Rauschel, hedge-bamboo, a native of southern China, persists after cultivation and sometimes spreads by rhizomes from plantings in central Florida (Judd, pers. comm.).

Members of subtribe Dendrocalaminae Benthham (including subtribe Melocanninae Benthham) are also tall bamboos. In contrast to the Bambusinae, this subtribe has fleshy fruits (drupes). The fruits of the Indian species *Melocanna baccifera* Roxb. are as large as pears and are baked and eaten. Certain species of *Melocanna* Trin. are cultivated in the West Indies.

Classification of bamboos has traditionally stressed vegetative features, and bamboo taxonomy has many terms specific to it. For example, two different kinds of rhizomes characterize bamboos. Leptomorph rhizomes are elongate, slender, and usually horizontal, while pachymorph ones are short, stout, and erect or oblique. The species of *Arundinaria* in the Southeast bear leptomorph rhizomes. Pachymorph species are clump formers, while leptomorph species produce single stems at close or distant intervals. *Arundinaria gigantea* forms close colonies, although the stems are not caespitose. Although bamboo stems elongate by intercalary meristematic activity, the relative lengths of the mature internodes contrast in different genera and species. In *A. Simonii* (Carr.) A. & C. Riv. the tenth internode of the stem is longest, while in *Bambusa multiplex* the fourth is longest. The order in which axillary branching begins falls into three broad patterns (McClure, 1966). In species of *Phyllostachys* and in *A. gigantea*, the direction is acropetal; in other species of *Arundinaria*, basipetal. In *Semiarundinaria viridis* Makino, branch initiation begins in the middle node and spreads upward and downward from there. Certain genera of bamboo produce more than one axillary bud at each node (termed constellate). In *Arundinaria* these buds produce branch complements that are again divided two or three times. Bamboos are the only grasses that have indeterminate inflorescences. The combination of stem elongation and branch initiation imparts the various architectural forms to mature bamboo plants.

The oryzoid grasses (tribe Oryzeae Dumort., including Zizanieae) have been treated as a subfamily, the Oryzoideae Parodi ex Caro. Since their affinities to the bambusoids are strong, they are included here in the Bambusoideae as they were by Campbell (1985), Dahlgren and colleagues, and Clayton & Renvoize. In addition to chromosomal ($x = 12$) and morphological (stamens 6 per flower; cross veins in leaves) similarities, the two groups have strikingly similar suites of amino acids in the endosperm (small amounts of glycine, proline, and phenylalanine and abundant threonine, alanine, valine, methionine, isoleucine, tyrosine, lysine, and arginine in comparison with other grasses; Yeoh & Watson). Oryzoid grasses differ from bambusoids in having stomata about equally distributed on both surfaces of the leaves instead of chiefly or wholly on the abaxial surface. Stomatal distribution of this kind is probably an adaptation to humid, sunny environments.

The Oryzeae, the members of which are herbaceous perennials or annuals, are characterized by one-flowered spikelets and glumes that are greatly reduced

or absent in several of the genera. The genera are clearly divided into three subtribes. The Oryzinae Reichenb. have perfect florets, while the Zizaniinae Honda and Luzioliinae Terrell & H. E. Robinson have imperfect ones. The Oryzinae (about eight genera worldwide, pantropic and warm-temperate) are represented in the Southeast by five native species of *Leersia* Sw. and the adventive *Oryza sativa* L.

The Zizaniinae are separated from the Luzioliinae by morphological, anatomical, embryological, and chromosomal features. Members of subtribe Zizaniinae have a base chromosome number of 15, laterally exerted stigmas, a typical grass caryopsis (pericarp fused to seed coat), an embryo with a narrow and free epiblast, and aerenchymatous leaf septa. The subtribe is unigeneric: *Zizania* has four species, three in eastern North America and one in eastern Asia. Members of subtribe Luzioliinae have a base chromosome number of 12, apically exerted stigmas, an achene (thickened pericarp surrounding but not adnate to seed coat), an embryo with a bilobed fused epiblast, and leaf aerenchyma not forming septa (see Terrell & Robinson for illustrations). *Zizaniopsis* Döll and *Luziola* Gmelin have stellate cells in the midribs (Renvoize). The subtribe includes about 16 species of tropical South America, the Caribbean region, and southeastern North America.

The ecology of members of subfamily Bambusoideae is diverse. There are annuals and perennials and woody and herbaceous species; there are mesic terrestrial and aquatic species but apparently no xeric ones. All genera have non-kranz anatomy and the C₃ photosynthetic pathway, both typical of plants of wet or shaded habitats.

Taxonomically important chemicals of the Bambusoideae are not strikingly different from those of other grass subfamilies; most of our information is derived from investigations of the economically important genus *Oryza* L. Cyanogenesis is reported in several genera (*Bambusa*, *Dendrocalamus*, *Leersia* Sw., *Melocanna*, and *Oryza*). Its effect on herbivory is apparently uninvestigated, but cattle have been poisoned by overeating sprouts of bamboos in India. Tannins are rare in the Bambusoideae; only *Phyllostachys aurea* is reported to contain them (Gibbs). Several flavonoids (the anthocyanins cyanidin and malvinidin, the glycosyl flavonoid carlinside, and the flavones tricrin and violanthin) occur in bambusoids, and all are reported from *Oryza sativa*. *Leersia oryzoides* Sw. (reported as *L. Sayanuka* Ohwi by Kaneta & Sugiyama) produces the flavones isovitexin, iso-orientin, and violanthin. The alkaloidal amine anhaline, the pyrrolidine *dl*-stachydrine, and the sterol satisterol have been reported from *Oryza sativa* (Gibbs).

The cytology of the Bambusoideae is rather uniform. All of our genera have chromosome numbers based on 12, except *Brachyelytrum* (11) and *Zizania* (15). Tetraploidy seems to be common in the Oryzaceae, especially in *Oryza*, where it is taxonomically significant. Worldwide, 81 percent of the genera of the woody bambusoids have numbers based on 12, 14 percent are based on 11, and the remainder on 10, 9, or 7 (Hunziker *et al.*). The woody bamboos are overwhelmingly polyploids, while the herbaceous bambusoids are primarily aneuploids. Only four percent of the woody bamboos (vs. 83 percent of herbaceous ones) are diploids. These karyotypic differences may well correlate

with contrasting life histories. Woody bamboos, with their long generation times and rhizomatous habit, have better opportunities for the perpetuation of autopolyploids than do herbaceous ones. Conversely, herbaceous bambusoids have annual flowering and much more chance for meiotic rearrangement leading to aneuploidy.

The reproductive biology of bambusoids has received some attention. Entomophily has been reported in certain tropical herbaceous species. Dioecy is unknown in the subfamily, and apomixis is unreported. Many species of the *Oryzaceae* and *Pharaceae* are monoecious, while the *Bambuseae* have perfect flowers. Self-compatibility, reported in *Pharus latifolius* (Judziewicz, pers. comm.), *Zizania*, and *Oryza*, seems to be more prevalent than in the other subfamilies of grasses. Certain species of *Leersia* (*Oryzaceae*) regularly produce inflorescences containing only cleistogamous spikelets.

The mass flowering and fruiting of many woody bamboos is a puzzling phenomenon, almost a study in itself. Numerous patterns of flowering have been observed; see McClure (1966, pp. 268–279) for a fascinating summary arranged by genus. The flowering cycle of *Bambusa polymorpha* Munro exceeds 80 years; in *B. arundinacea* Willd. it is about 50 (Arber, 1934). In our native southeastern species, colonies of *Arundinaria tecta* flower every four or five years, those of *A. gigantea* every 40–50. Some species remain vegetative for years, and some are not known ever to have flowered either in the wild or in cultivation. Many species (e.g., *Chimonobambusa quadrangularis* (Fenzl) Makino and *Sasa tessellata* (Munro) Makino & Shibata) are monocarpic and die after flowering, while others (e.g., *Bambusa lineata* Munro) flower annually. *Bambusa tuldoidea* Munro dies after flowering in its native China, but cultivated plants in Central America flower continuously for years. The number of years until flowering is evidently a genetically controlled character (Janzen), as is suggested by numerous reports of transplanted populations that flower at the same time as clones in geographically distant areas. For example, *Chusquea abietifolia* Griseb. was introduced to the island of Jamaica, where it was extensively propagated by division. One of these divisions was the source of a cultivated stand in the Botanic Gardens at Kew, England. In 1884–1885 all the plants of this species in Jamaica, as well as those at Kew, flowered and died. Drought and disturbance by cutting have been suggested as causes for local flowering of bamboo populations, but the data are not conclusive. The evolutionary origins and adaptive significance of long generation times in the woody bamboos offer great possibilities for further research.

Several patterns of dispersal are represented in the subfamily. Species of tribe *Pharaceae* bear fruits enclosed in lemmas with hooked trichomes that are presumably involved in dispersal by birds and mammals, possibly explaining the pantropic distribution of *Pharus*. In *Zizania palustris* L. the bristly awn of the lemma anchors the enclosed caryopsis to the bottom of the lake or stream, stabilizing it against movement by waves or currents until the root system develops. The fleshy fruits of certain woody bamboos (e.g., *Melocanna*) are as large as pears and fall to the ground beneath the parent. Most are eaten by herbivores, and few survive to germinate. Fruits of *M. bambusoides* Trin. are

viviparous. The hypocotyl and radicle emerge before the small, fleshy caryopsis drops from the parent plant.

The economic importance of certain species of this subfamily is great. Rice is the major food for half the world's population. Woody bamboos provide material for construction in Asia, Africa, and Latin America. Many species of bamboo are cultivated for their edible shoots, a familiar part of Oriental cuisine. Numerous species of woody bamboos are cultivated throughout tropical and warm-temperate regions as ornamentals (see McClure, 1957, 1966, 1973, for an account of those cultivated in the United States, and Lawson for horticultural information). Wild rice (*Zizania*) is extensively gathered for food in North America. Further information on economic importance appears in the generic accounts.

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KEY TO THE GENERA OF BAMBUSOIDEAE IN THE
SOUTHEASTERN UNITED STATES

General characters: *herbs or shrubs of woods, streambanks, wetlands, and lakes (sometimes submersed or emergent); stems leafy; sheaths open; ligules present, glabrous or hairy; blades sessile or petiolate, the primary veins parallel to or slightly divergent from midvein, secondary veins usually present and perpendicular to main veins, giving the blades a tessellate appearance; inflorescences paniculate; spikelets several to many, 1- to few-flowered; glumes 1 or 2 or lacking; lemmas elliptic to lanceolate; flowers perfect or imperfect; lodicules sometimes present; stamens 2-6; stigmas 2 or 3, usually plumose; fruit a caryopsis or an achene, often firmly clasped by the persistent palea and lemma.*

- A. Stems woody, perennial.
- B. Branches solitary at each node of main stem. [*Pseudosasa*.]
- B. Branches 2 to several at each node of main stem.
- C. Stems flattened on one side above each node; leaf scar a distinct line beneath node. [*Phyllostachys*.]
- C. Stems terete; leaf scar on node.
- D. Stems sometimes thorny; lemmas glossy; stamens 6 per flower. [*Bambusa*.]
- D. Stems unarmed; lemmas dull; stamens 3 per flower. . . 1. *Arundinaria*.
- A. Stems herbaceous, annual.
- E. Leaf blades petiolate, the primary veins diverging 5-10° from midvein; lemmas densely covered with uncinata to clavate trichomes. 2. *Pharus*.
- E. Leaf blades sessile, the primary veins all parallel to the midvein; lemmas smooth or scabrous.
- F. Rachilla prolonged above base of palea, bristlelike, ½ as long as palea. 3. *Brachyelytrum*.
- F. Rachilla not prolonged above base of palea.
- G. Flowers perfect.
- H. Rhizomes absent, plants annual; spikelets subterete; 2 lower lemmas lanceolate, the fertile one elliptic, commonly awned; stamens 6. 4. *Oryza*.
- H. Rhizomes usually present, plants perennial; spikelets strongly flattened laterally; 2 lower lemmas minute, the fertile one lunate, awnless; stamens 2, 3, or 6. 5. *Leersia*.
- G. Flowers imperfect.
- I. Stems stout; plants tall emergents of shallow waters; carpellate and staminate spikelets on same or different primary branches of the same inflorescence.
- J. Non-rhizomatous annuals; staminate and carpellate flowers on separate inflorescence branches, the carpellate branches distal to the staminate. 6. *Zizania*.
- J. Rhizomatous perennials; staminate and carpellate flowers on same inflorescence branches, the carpellate spikelets distal to the staminate. 7. *Zizaniopsis*.
- I. Stems slender; plants small, submersed or littoral; carpellate and staminate spikelets in separate, few-flowered inflorescences. 8. *Luziola*.

Tribe BAMBUSEAE Dumortier, Anal. Fam. Pl. 63. 1829, "Bambusaceae."

1. *Arundinaria* Michaux, Fl. Bor.-Am. 1: 73. 1803.

Large, woody perennials of damp thickets, pocosins, brushy pastures, swamp margins, and stream banks. Rhizomes slender (leptomorph), horizontal, extensively creeping, sometimes with air chambers. Stems solitary to caespitose, erect; branches borne in the axils of the leaf sheaths; nodes glabrous. Leaves 10–20; sheaths papery, equaling or shorter than the corresponding internode, closely fitting the stem, persistent or deciduous; ligules bearing several short bristles, deciduous; blades dimorphic, the basal 6–10 leaves bearing linear blades much shorter and narrower than their sheaths, the distal ones bearing narrowly elliptic, petiolate blades with parallel veins and transverse veinlets. Inflorescences open, racemose or paniculate, with first-, second- (and sometimes third-) order branching. Spikelets 4- to 12-flowered, large, dorsiventrally compressed, disarticulating above the glumes. Glumes (1 or) 2 (or 3), unequal, narrowly elliptic, acute, more or less mucronate, shorter than the lowest lemma. Lemmas 4–12, elliptic, [acute, mucronate, or] aristate, 11-nerved. Paleas elliptic, equaling or slightly shorter than the lemmas, acute, 2-nerved, sulcate between the 2 nerves. Lodicules 3 (the adaxial one usually adhering to the palea, easily overlooked), oblong-elliptic, obtuse, 5- to 7-nerved, ciliate abaxially and sometimes marginally also. Flowers perfect. Stamens 3; filaments filiform; anthers linear, the apex of the connective not prolonged. Ovaries broadly obovoid, glabrous. Styles glabrous, much shorter than the stigmas; stigmas 3, aspergilliform (brushlike from long, glandular papillae). Caryopsis narrowly ellipsoid, terete, sometimes with uncinatate beak, glabrous. Base chromosome number 12. TYPE SPECIES: *A. macrosperma* Michx. (= *A. gigantea* (Walter) Muhl. subsp. *macrosperma* (Michx.) McClure or *A. gigantea*), the only species treated by Michaux. (Name from Greek *arundo*, reed.)

A genus of some 50 species (Clayton & Renvoize), all confined to the Old World (McClure, 1973) except *Arundinaria gigantea*, $2n = 48$, and *A. tecta* (Walt.) Muhl., which are endemic to southeastern North America. *Arundinaria gigantea* ranges from southern Delaware to southern Ohio, south to Florida and eastern Texas (McClure, 1973). *Arundinaria tecta* occurs chiefly on the Coastal Plain and Piedmont from eastern Virginia to southern Alabama. Both species form thickets called "cane brakes" along streams and in moist woods. *Arundinaria tecta* becomes more abundant in response to frequent fires in pocosins and savannas, and it can become an understory dominant (Wells & Whitford).

Taxonomic variation in the North American representatives has been variously interpreted. At least two taxa are present. McClure (1973) treated these as subspecies of *Arundinaria gigantea*, but it seems justifiable to treat them as species, since they differ by as many features as do Japanese species of the genus in Ohwi's conservative account. The American *A. gigantea* and *A. tecta* differ in several morphological features,³ have different ranges, and have apparently different phenologies (Fernald & Kinsey) but the same chromosome

number. *Arundinaria gigantea* flowers every 40–50 years, *A. tecta* every 3–4. A third taxon, *A. macrosperma* Michx. (*A. gigantea* subsp. *macrosperma* (Michx.) McClure), was believed by McClure (1973) to be derived from hybridization and introgression of the two preceding species.

Arundinaria japonica Sieb. & Zucc. is “doubtfully escaping” in southern Florida (Long & Lakela).

Arundinaria Simonii (Carr.) A. & C. Riv. (*Pleioblastus Simonii*), $2n = 48$, is widely cultivated in western Europe and also in the southeastern United States. The plants are curious in that the left and right halves of the lower surface of the leaf blades are unlike in the distribution of papillae (Jones & Hermes). The half with more papillae appears darker to the naked eye and is outermost when the leaf is rolled in bud (Clayton & Renvoize).

The stems and leaves of *Arundinaria tecta* are good forage for cattle. The formerly extensive cane brakes of eastern Texas have been greatly reduced by the expansion of cattle ranching.

Stems of *Arundinaria amabilis* McClure, Tonkin cane, are used for making fly-fishing rods. The smaller stems are used for florists' stakes.

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⁵The two species are distinguished as follows, using characters given by McClure (1973, p. 25) checked against specimens examined in this study:

- Rhizomes lacking air canals; midstem sheaths shorter than the corresponding internode; leaf blades glabrescent above; lemmas hirsute, greenish, transverse veinlets clearly visible; lodicules translucent, marginally ciliate; ovary and caryopsis without hooked apex. *A. gigantea*.
- Rhizomes with longitudinal air canals; midstem sheaths longer than corresponding internode; leaf blades pubescent above; lemmas glabrous, reddish tinted, transverse veinlets inconspicuous; lodicules transparent, entire; ovary and caryopsis with hooked apex. *A. tecta*.

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Tribe PHAREAE Stapf in Thiselton-Dyer, Fl. Capensis 7(2-4): 319. 1898.

2. **Pharus** P. Browne, Civ. Nat. Hist. Jamaica, 344. tab. 38, fig. 3. 1756.

Perennials of moist subtropical [tropical] forests and woodlands. Rhizomes lacking; stems decumbent, rooting at the lower nodes, covered (or nearly so) by the overlapping leaf bases. Leaves several; sheaths about as long as the blades, open for over 1/2 their length, glabrous; ligules wider than long, apically fimbriate; petioles resupinate (abaxial surface of blade uppermost in the third and succeeding leaves); blades elliptic, acuminate [acute], glabrous, the lateral veins forming an angle of 5-10° with the main vein, numerous transverse veinlets connecting the lateral veins, giving the leaf surface a tessellate appearance. Inflorescences terminal, paniculate, the primary branches nearly horizontal, scabrous and/or hispidulous throughout, secondary branches often present. Spikelets 1-flowered, ellipsoid, imperfect, the staminate ones about 1/2 as long as the carpellate and borne singly on short pedicels from the axils of the carpellate spikelets. Glumes 2, subequal, broadly lanceolate, shorter than the lemmas, nerveless, glabrous. Lemma 1, narrowly elliptic, margins inrolled around the flower, surface densely covered with stiff, clavate to uncinat trichomes. Palea narrowly elliptic to lanceolate, shorter than lemma (lacking in staminate spikelet). Stamens 6; filaments filiform, slightly shorter than the lemmas; anthers linear, the apex of the connective not prolonged. Ovaries narrowly elliptic, glabrous; styles terete basally, becoming flattened distally; stigmas shorter than style, sparsely glandular, exerted at same time as anthers. Caryopsis cylindrical, oblong. Embryo small, basal. Base chromosome number 12. TYPE SPECIES: *P. latifolius* L., the only species treated by Browne (with a polynomial) and named validly (1759) by Linnaeus. (Name from Greek *pharos*, mantle, possibly alluding to the broad leaf blades).—CREEPING LEAFSTALK GRASS.

A Neotropical genus of seven species (Judziewicz, 1985b), represented in the southeastern United States by *Pharus lappulaceus* Aublet. This species occurs from northern and central Florida and eastern Mexico (San Luis Potosí) south through the West Indies and Central America to Uruguay and Argentina (Prov. Tucumán). It has the widest range of any species of *Pharus*, covering nearly the entire range of the genus. It has not been collected in Florida since 1921 (Small et al. 10084, NY, US; *vide* Judziewicz, 1985b) and is probably extirpated in the United States.

Chromosome numbers of $2n = 24$ have been reported for *Pharus glaber* HBK. (Pohl & Davidse) and *P. latifolius* (Reeder).

No economic uses have been reported for the genus, and apparently no species

is a significant weed. In the original description of the genus, Browne noted that the plants were eaten by cattle in Jamaica. Grazing has been suggested as a cause of the disappearance of *Pharus lappulaceus* in Florida.

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REEDER, J. R. In: IOPB chromosome number reports XXII. *Taxon* 18: 433–442. 1969.

Tribe BRACHYELYTREAE Ohwi, *Bot. Mag. Tokyo* 55: 361. 1941.

3. *Brachyelytrum* Palisot de Beauvois, *Essai Agrost.* 39. 1812.

Small perennials of temperate, mesic to wet-mesic forests. Rhizomes short, horizontal, covered with cucullate to lanceolate scales. Stems erect, 1–4; nodes retrorsely hispid. Leaves 2–5; sheaths sparsely retrorsely hispid; ligules broadly oblong, hyaline; blades lanceolate-linear, flat, pilose on the nerves abaxially, scabrous on both surfaces generally, primary veins parallel, secondary veins transverse to slightly oblique. Inflorescences terminal, narrowly paniculate; nodes glabrous; branches erect, scabridulous. Spikelets few, 1-flowered, pedicellate; rachilla bristlelike, about $\frac{2}{3}$ as long as the lemma. Glumes 2, unequal, lanceolate (the second sometimes aristate), much shorter than the lemma. Lemma lanceolate, 5-nerved, acute, bearing a long, scabrous, apical awn, the base contracted to a scabrous, indurate callus, the surface scabrous (the nerves sometimes hispid). Palea lanceolate, slightly shorter than the lemma. Stamens 3; filaments filiform, nearly as long as the palea; anthers linear, the connectives not prolonged. Ovaries slenderly conical, bristly; styles very short, glabrous; stigmas 2, stipitate-glandular. Caryopsis firmly enclosed by lemma and palea, oblong, subterete, with bristly apex and spongy beak, the adaxial surface grooved. Base chromosome number 11. TYPE SPECIES: *B. erectum* (Schreber) Beauv. (*Muhlenbergia erecta* Schreber), the only species included in the genus by Palisot de Beauvois. (Name from Greek *brachys*, short, and *elytron*, husk, referring to the minute glumes.)

A genus of three species exhibiting the classic disjunction between eastern North America and temperate eastern Asia. *Brachyelytrum erectum* occurs throughout our area and northward to Massachusetts, central New York, Ohio, southern Michigan, and southern Wisconsin. *Brachyelytrum septentrionale* (Babel) G. Tucker⁶ occurs from Newfoundland to Minnesota south to northern

⁶*Brachyelytrum septentrionale* (Babel) G. Tucker, comb. nov., based on *Brachyelytrum erectum* (Michx.) Beauv. var. *septentrionale* Babel, *Rhodora* 45: 260. 1943. TYPE: New Hampshire, Strafford County, Durham, *Babel* 46 (holotype, wis; isotypes, f!, GH!). (Not including *B. aristosum* var. *glabratum* Vasey ex Millsp., *Bull. W. Virginia Exper. Sta.* 24: 469. 1892. TYPE: West Virginia, Fayette County, Nuttallburg, 1890. *L. W. Nuttall s.n.* (holotype, f, accession no. 100250!), which is a plant of *B. erectum*, not *B. septentrionale* as stated by Koyama & Kawano.)

New Jersey, West Virginia, western North Carolina (Jackson County, below Tuckasee Falls, *H. F. Williams s.n.*, 7/6/31, DUKE!, F!), southern Michigan, and central Wisconsin. Stephenson examined the populations of both species in Michigan and found consistent morphological differences. He indicated that further study throughout North America is necessary to confirm that these two taxa are indeed species, as is indicated by their distinctiveness in Michigan. I have examined specimens from throughout eastern North America and find that the two taxa can be easily and consistently separated by his criteria; *B. erectum* has few (5–10(–20) per cm) cilia (macrohairs) on the leaf margins and stiff hairs 0.4–0.6 mm long on the lemmas; *B. septentrionale* has abundant ((30–)40–60 per cm) cilia on the leaf margins and lemma hairs only 0.1–0.2 mm long. There are also differences in the lengths of the palea (10–12 mm in *B. erectum*, vs. 8–10 mm in *B. septentrionale*), the second glume (1.5–2.5 (–4.5) vs. 1–1.5(–2) mm), and the anthers (5–6 mm vs. 2.5–4(–5) mm). The length of the rachilla (6–7 mm vs. 5–6.5 mm) overlaps too much to be used alone. In areas of sympatry (e.g., central New York), about five percent of the collections appear to be intermediates of hybrid origin. Stephenson noted the occurrence of apparent hybrid populations in southern Michigan.

The two species of *Brachyelytrum* are nearly allopatric in Pennsylvania, with *B. septentrionale* occurring in moist woods in the northern half of the state and *B. erectum* in mesic woods in the southeastern third (Pohl). In Wisconsin *B. erectum* has a more southerly distribution than *B. septentrionale* (Fassett). In southern Michigan, where both species are found, *B. septentrionale* flowers about ten days before *B. erectum* (Stephenson). Stephenson reported that anthesis within populations of both taxa was highly synchronous. As far as he could determine, it was confined to the first half of the morning of a single day.

Brachyelytrum japonicum Hackel, $2n = 22$, differs from the North American species in having narrower leaf blades and longer glumes (Koyama & Kawano). It occurs in southern Japan, Korea, and east-central China.

Hackel (1897) also included three tropical species in the genus. These were *Brachyelytrum procumbens* Hackel (northern South America), of subg. *Aphanelytrum* Hackel, and *B. aristatum* (Beauv.) Hackel and *B. silvaticum* (K. Schum.) Hackel (East African mountains), of subg. *Pseudobromus* (K. Schum.) Hackel. Plants of subg. *Aphanelytrum* have 2- or 3-flowered spikelets. Hackel later elevated this taxon to generic status, an opinion shared by Chase (1916), who considered it a member of tribe Festuceae Dumort. (= Poaeae). Clayton & Renvoize placed this monotypic genus in tribe Poaeae but did not comment on its previous placement in *Brachyelytrum*. They treated *Pseudobromus* K. Schum. as a synonym of *Festuca* L. (tribe Poaeae), similarly without mention of its inclusion in *Brachyelytrum* by Hackel.

Plants of *Brachyelytrum* have no reported economic importance. No species are reported as weeds.

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Tribe ORYZEAE Dumortier, *Obs. Gram. Belg.* 83. 1824.

Subtribe **Oryzinae** Reichenbach, *Deutschlands Fl.* **5**: 6. 1846, "Oryzeae."

4. **Oryza** Linnaeus, *Sp. Pl.* **1**: 333. 1753; *Gen. Pl.* ed. 5. 29. 1754.

Annuals [perennials] of ditches, shores, marshes, and other open freshwater [brackish] wetlands. Rhizomes lacking [present]. Stems erect (sometimes ascending, rooting at the lower nodes if submersed), single or caespitose by tiller formation; nodes glabrous. Leaves several per culm; sheaths open for much of their length, glabrous; ligules broadly lanceolate, scabrous abaxially; blades linear, flat, surface glabrous, veins parallel, transverse veinlets lacking, basal auricles sometimes present. Inflorescences terminal, paniculate; branches flexuous and slightly drooping, glabrous generally but axils sometimes pilose. Spikelets 1-flowered, more or less persistent [promptly deciduous]; rachilla not prolonged beyond palea. Glumes 2, greatly reduced, forming a cupulate structure at base of spikelet. Lemmas 3, the 2 basal ones lanceolate [linear], weakly nerved, glabrous, sterile, the fertile one elliptic [ovate], stiffly conduplicate, 5-nerved, acute, mucronate or bearing an awn up to 10 times as long as the body of the lemma, the abaxial surface papillose, glabrous, scabrous, or hirsute. Palea lanceolate, mucronate, 2-nerved submarginally, edges hyaline. Flowers perfect. Stamens 6; filaments filiform; anthers narrowly ellipsoid, the apex of the connectives not prolonged. Ovaries ellipsoid, glabrous, bearing an apiculate appendage adjacent to the style base; styles glabrous; stigmas 2, longer than the styles, aspergilliform, exerted laterally (1 on each side of the lemma), before the anthers. Caryopsis narrowly [to broadly] ellipsoid, cylindrical to compressed, enclosed by the sclerified lemma and palea. Base chromosome number 12. TYPE SPECIES: *O. sativa* L., the only species included by Linnaeus. (Name from Greek *oruzá*, rice, derived from Arabic *eruz*, rice.)—RICE.

A pantropic and warm-temperate genus of 18 species (Duistermaat). About 12 species are found in southeastern Asia and Australia, the center of diversity for the genus; six occur in Africa, and three are native to the New World. The genus is well known and economically significant because of *Oryza sativa* L., rice, one of the world's two most important crops.

Oryza is closely related to *Leersia*, but the two genera can easily be distinguished since *Leersia* lacks the two sterile lower lemmas consistently present in species of *Oryza* (see additional comments under *Leersia*). The genus consists of three sections (Tateoka, 1962a, 1962b, 1963) that differ in morphology, embryology, and cytology. Section ORYZA (sect. *Sativae* Roshev.; sect. *Euryza* Baillon) is characterized by embryos in which the epiblasts are laterally fused to the scutellum and lateral outgrowths (auricles) of the lower scutellum fill the space between the epiblast, the coleoptile, and the ventral scale. Such embryos with auricles are not known elsewhere in the Gramineae (Tateoka, 1964). Section ORYZA is composed of two series (Nayar; Sharma & Shastri, 1965). Members of series ORYZA (series *Sativa* Sharma & Shastri) are caespitose annual or perennial plants of wetlands, forming large, gregarious populations. There are five species, all diploids, $2n = 24$, of pantropic distribution (Nayar). They have genome AA, according to the system of Morinaga & Kuriyama. One species, *Oryza sativa*, is cultivated worldwide in tropical and warm-temperate regions. It is adventive in the southern United States (South Carolina to Texas), the Sacramento Valley of California, and various localities in the Neotropics south to northern Argentina. *Oryza glaberrima* Steudel, native to West Africa, is adventive in El Salvador (Adair *et al.*) and in northern South America. Other species of this series are *O. rufipogon* Griff., a pantropic species that is probably the nearest relative of *O. sativa*, *O. longistaminata* A. Chev. & Roehr., *O. Barthii* A. Chev. (*O. Stapfii* Roshev.), and *O. meridionalis* Ng, an endemic of Australia.

Series LATIFOLIAE Tateoka (sect. *Officinalis* Richharia) includes ten species and has a pantropic distribution. The plants are tall aquatic perennials with large, open panicles. All are tetraploids, $2n = 48$. Seven species, the most widespread of which are *O. minuta* Presl and *O. punctata* Steudel, occur in the Old World. These species have genome BBCC, whereas those from the New World have CCDD. The three remaining species are Neotropical: *O. latifolia* Desv., $2n = 48$, of the West Indies and Central and South America; *O. grandiglumis* (Döll) Prodöhl, $2n = 24, 48$, of the Amazonian region of South America; and *O. alta* Swallen, of Central and South America. These species, similar in habit, differ chiefly in features of the spikelets. All of the New World species were treated as varieties of *O. latifolia* by Chevalier.

Section RIDLEYANAE Tateoka includes two species, *Oryza Ridleyi* J. D. Hooker, of southeastern Asia, and *O. longiglumis* Janzen, of New Guinea. The plants are vigorous rhizomatous perennials, the spikelets have setaceous sterile lemmas, and the keels of the fertile lemmas are hirsute. The caryopsis is oblong and glabrous, the embryo lacks auricles, and the epiblast is laterally free from the scutellum (Tateoka, 1964). The genomic constitution apparently is unknown (Nayar).

Section GRANULATAE Roshev. (*Padia* (Zöll. & Mor.) Baillon) is monotypic. The plants have sparse, contracted panicles with fewer than 20 spikelets, and the lemmas are muticous. Embryologically it is like sect. RIDLEYANAE. The plants are caespitose and grow in woodlands in dry to damp soils. The genomic relations are unknown. The only species, *Oryza Meyeriana* (Steudel) Baillon (including *O. Abromeitiana* Prodöhl), of southern and southeastern Asia, consists of two subspecies, subsp. *Meyeriana* and subsp. *granulata* (Watt) Dui-

stermaat, both $2n = 24$, that differ in the shape of the spikelets. The fossil *O. exasperata* (A. Br.) Heer, of the Miocene strata of Germany, is very similar to *O. Meyeriana* (Duistermaat).

Roshevitz recognized a fourth section, *Coarctatae* Roshev., in his monograph of the genus. On anatomical and embryological grounds, Tateoka (1964) has treated this as *Sclerophyllum* Griff. Its only species, *S. coarctatum* (Roxb.) Griff. (*Oryza coarctata* Roxb.), is endemic to India.

The cultivated forms and varieties of *Oryza sativa*, named and unnamed, number in the thousands. They are generally grouped into three subspecies: subsp. *sativa*⁷ (subsp. *indica* Kato), grown primarily in India and Burma; subsp. *japonica* Kato, grown in China and Japan; and subsp. *javanica* Matsuo, of Indonesia. The typical subspecies ("Indica rice") sheds its spikelets most readily; subsp. *javanica* generally has awned spikelets, while both subsp. *sativa* and subsp. *japonica* are awnless. There are chemical and physiological differences as well. Only in subsp. *sativa* does the endosperm react with phenol, giving a reddish color. Subspecies *japonica* has a greater tolerance for anaerobic germination than do the other subspecies, including wild populations. There are thousands of cultivars. Most American cultivars are derivatives of subsp. *javanica* (Adair *et al.*).

Oryza sativa is usually an annual, but some cultivars can be perennial, at least in tropical regions. In wild races of *O. sativa* (by some workers treated as *O. rufipogon*), the mature grains drop into mud or water, but they are internally dormant and do not germinate until the next rainy season (Arber, 1934). The dormancy is not overcome by chilling, but a dry treatment at 40–50°C for one to two weeks produces good germination. Stratification is also effective. Seeds buried in mud for several weeks will germinate when exposed to oxygen. Seeds can remain viable but dormant in damp soil for several years. In certain cultivars dormancy of seeds can be influenced by high temperatures or high moisture affecting the parent plants at the time of pollination.

Cultivars of *Oryza sativa* cross-pollinate with wild or weedy races of the species and perhaps also with plants of *O. rufipogon* in southeastern Asia. Hybrids can be made by simply tying together the panicles of the desired parental plants. Such hybrids introgressed with cultivated strains of *O. sativa*, yielding genetic combinations that have been propagated as new cultivars.

All species reported have chromosome numbers of either $2n = 24$ or $2n = 48$. *Oryza sativa*, $2n = 24, 48$, is well known cytologically and genetically. Four of its 12 chromosomes are sub-metacentric; the others telocentric. The longest chromosome is about twice as long as the shortest. The genes are mapped onto 12 linkage groups corresponding to the 12 chromosomes of the haploid karyotype. Morphologically or chemically related traits are generally not located within the same linkage groups. The loci controlling dormancy are several, and their interaction is complex. The anthocyanin coloration of the apiculus of the lemma is governed by three loci and 20 alleles. An additional locus controls the golden vs. white coloration of the furrows of the lemmas. Additional genes determine the brown or red color of the pericarp. Awn length is governed by

⁷In botanical and agricultural literature this is called subsp. *indica* Kato, "Indica rice." This is, however, a botanical rank, and the autonym rule applies. The type specimen of *O. sativa* came from India and was evidently a cultivated plant of the Indica type.

the interaction of three loci, each located on a different chromosome. The presence or absence of hairs on the lemmas is controlled by a single locus. Two additional ones can lead to lemmas with dense, long hairs. A detailed summary of the genetics of rice with interesting details of inheritance is given by Tsunoda & Takahashi.

As noted above, *Oryza sativa* is most closely related to the pantropic *O. rufipogon*. It is generally believed that cultivated subspecies of *O. sativa* evolved from annual wild progenitors over a broad area from the foothills of northern India to northern Vietnam and southernmost China. This apparently occurred independently and concurrently at a number of sites. "Weed rice" (intermediate between cultivated and wild races) is known from as early as 3500 B.C. from archeological sites in northern Thailand. Carbonized "glumes" (i.e., lemmas) indicate that the plants were gathered or possibly cultivated at that time. Rice was first cultivated in China about 3000 B.C. and in India about 1500 B.C. The Chinese pictograph for rice first appeared about 1500 B.C.; by the first century A.D. several cultivated varieties of rice were mentioned in Chinese literature. Subspecies *sativa* (*indica*) originated in northeastern India and from there was introduced to Malaysia and Taiwan; subsp. *javanica* was developed in Indonesia by 100 B.C. (perhaps earlier) and brought into the Philippines and Japan; and subsp. *japonica* was domesticated in China and introduced to Korea and Japan about the third century B.C. Using electrophoretic data, Second (1986) showed that the distinction between subspecies *sativa* and *japonica* is a natural one, probably a result of allopatric subspeciation between northern and southern populations of wild rice separated by the uplift of the Himalayas.

Oryza glaberrima, the cultivated rice of West Africa, was domesticated from wild populations of the same species (Second, 1986) in swampy areas of the upper Niger Basin of tropical West Africa. Selection began as early as 1500 B.C. *Oryza sativa* was introduced to West Africa in the seventeenth century. In West Africa today *O. glaberrima* and *O. sativa* are customarily grown together in about equal amounts. About 75 percent of West African rice is cultivated in the uplands (while most Asian and American rice is cultivated in inundated soils).

Differences between cultivated and wild strains of rice are similar to those between artificially selected and wild types of other cereal crops, as a result of similar human selection. Cultivated varieties are larger plants and have greater growth rates than wild races. They also have strongly synchronized germination, growth, and seed set within populations. The panicles and spikelets are more persistent and thus do not shatter, a feature that facilitates harvesting. Cultivated plants differ in loss of pubescence on foliage and lemmas and in loss of awns (in certain varieties), and they have shorter anthers and larger, heavier grains. They have less pigmentation, and their karyotypes are more asymmetric at pachytene than those of wild races.

Oryza sativa is a weed in some 30 tropical and warm-temperate countries (Holm *et al.*). The weedy, spontaneous plants are called red rice (because of the reddish spikelets and grains) and are a major weed of American rice fields (Adair *et al.*). Several other species (e.g., *O. rufipogon*) are weeds, particularly in southeastern Asia.

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5. *Leersia* Swartz, Prodr. Veg. Ind. Occ. 21. 1788, nom. cons.

Perennials [annuals] of damp woods, shores, ditches, and rice fields. Rhizomes stiff, horizontal, closely covered with firm, cucullate scales. Stems loosely clustered, erect or decumbent, terete or slightly compressed (sometimes rooting at the lower nodes); nodes glabrous or shortly hirsute. Leaves several, the lowermost sometimes bladeless; sheaths scabrous (sometimes also pubescent), open for much of their length; ligules truncate [broadly lanceolate], 1[–2] times as high as the width of the blades, glabrous, becoming erose with age; petioles short; blades flat to plicate [involute], auriculate, the margins (and sometimes the surfaces) scabrous (the prickles extrorse or retrorse). Inflorescences terminal (smaller axillary ones sometimes present, the lower branches or the entire inflorescence sometimes enclosed within the sheath of the subtending leaf), panicate; branches 1–4 per node, ascending to spreading, secondary branches frequently present as well. Spikelets 1-flowered, ellipsoid to oblong, strongly flattened. Glumes reduced to a tiny cupulate structure at base of spikelet. Lemma 1, lunate, stiffly conduplicate, acute [contracted into a cauda (“pseudo-down”) as long as body of lemma], 5-nerved, glabrous or hispid on the abaxial surface or only on the nerves, the keel scabrellate or ciliate. Palea 1, broadly lanceolate, conduplicate, about as long as lemma, acute, sometimes mucronate, 3-nerved (the middle nerve more conspicuous than the lateral ones, ciliate or scabrellate), the margins straight. Flowers perfect. Lodicules 2, ovate, obtuse

[emarginate], hyaline, 3-nerved. Stamen(s) [1,] 2, 3, or 6; filaments filiform; anthers linear to oblong, the apex of the connectives not prolonged. Ovaries slenderly ellipsoid, glabrous; styles glabrous, very short [absent]; stigmas 2, plumose, exerted with or after the anthers. Caryopses gibbous (adaxial edge straight, abaxial edge broadly convex), flat to subterete. Base chromosome number 12. (*Homalocenchrus* Mieg, *Acta Helvetica* 4: 307. 1760, nom. rejic.) TYPE SPECIES: *L. oryzoides* (L.) Sw. (*Phalaris oryzoides* L.), typ. cons. (Named for Johann Daniel Leers, 1727-1774, German botanist and pharmacist.)—CUTGRASS, WHITEGRASS, CATCHFLY GRASS.

A genus of 17 species, worldwide in warm-temperate and tropical regions. The center of diversity is tropical Africa, where eight species (seven of them endemic) occur. *Leersia triandra* is endemic to West Africa, two species are found only in eastern Asia, and two occur in Central and South America. Five species (two of them endemic) grow in North America; all are present in the Southeast.

Lauert studied the African species, and Pyrah examined the remaining ones. The genus is, however, in need of a thorough worldwide revision. *Leersia* consistently lacks the two sterile lower lemmas present in all species of *Oryza*, but there has been some confusion of generic limits. Certain African and Asian species of *Leersia* have "awned" lemmas, but these structures are not homologous with the awns of *Oryza* species. The awns of *Leersia* have three vascular bundles, while those of *Oryza* have only one. In *Oryza* the vascular bundles in the lateral nerves of the lemmas end in a pair of mucros at the base of the true awn. In those species of *Leersia* with "awns," the two lateral nerves join the bundle of the midvein and continue into the caudate apex of the lemma (Lauert; Pyrah). Confusion about the "awns" of certain *Leersia* species has resulted in their inclusion in *Oryza* by some workers.

The possession of one, two, three, or six stamens by species of a single genus is an uncommon condition noted in few if any other genera of grasses. The studies of Holm (1892, 1895) and Pyrah pointed out two groups in the genus based on concordance of stamen number and leaf anatomy. It seems appropriate to treat these groups as sections. Section HEXANDRAE G. Tucker⁸ has six stamens per flower and groups of bulliform cells distributed on both surfaces of the leaf blades. Several African species with caudate ("awned") lemmas form a distinct group within sect. HEXANDRAE. The only New World species of this section is *Leersia hexandra* Sw. (plants rhizomatous, spikelets oblong, keels ciliate), $2n = 48$, a pantropic and warm-temperate species. It is known in North America from southeastern Virginia to Florida and Texas and from central Tennessee.

The four remaining North American species of the genus belong to the more advanced section LEERSIA. They have one to three stamens, and the bulliform cells occur only on the upper surface and in two small patches near the midvein on the lower surface. This section can be divided into two informal groups:

⁸*Leersia* section *Hexandrae* G. Tucker, sect. nov. *Leersiae* rhizomatosae; cellulae bulliformes in superficiebus ambabus folii; stamines sex.—SPECIES TYPICUS: *L. hexandra* Swartz.

caespitose plants of mesic to dry habitats, and rhizomatous ones of damp soils and shallow water. *Leersia oryzoides* (L.) Sw. (plants rhizomatous, spikelets ellipsoid, stamens 3), $2n = 48$, has the widest range, occurring throughout the United States and southern Canada. It is also reported from western Europe, central Asia, and Japan. *Leersia virginica* Willd. (plants rhizomatous, spikelets ellipsoid, stamens 2), white-grass, $2n = 48$, is widespread in eastern North America from New Hampshire, southern Quebec, and North Dakota south to northern Florida and eastern Texas. *Leersia lenticularis* Michx. (plants rhizomatous, spikelets suborbiculate, keels ciliate, stamens 2), catchfly-grass, $2n = 48$, is endemic to the southeastern Coastal Plain and Mississippi drainage, occurring from eastern Virginia, Illinois, and Minnesota to western Florida and eastern Texas. *Leersia monandra* Sw. (plants lacking rhizomes; spikelets ovate, glabrous; stamens 2), $2n = 48$, a species of the Caribbean basin, is known in the United States only from southern Florida and southern Texas. The nearest relative of *L. monandra* is the Neotropical *L. ligularis* Trin. (see Pyrah). In late Miocene times the now-extinct *L. nebraskensis* (J. Thomasson) G. Tucker,⁹ a species most closely resembling *L. ligularis*, occurred in the Great Plains of western Nebraska (Thomasson). This is the earliest record of fossil material of *Leersia*, and indeed of the Oryzaceae. *Leersia nebraskensis* grew in a mesic lacustrine community and thus differed ecologically from *L. ligularis* and *L. monandra*, both of which inhabit open rocky woods.

Leersia oryzoides includes plants with either cleistogamous or chasmogamous spikelets (Arber, 1934; Fogg). In the plants bearing cleistogamous spikelets, the panicles remain within the subtending leaf sheath and seed set is high; in the chasmogamous ones the panicles are exserted and seed set is lower. Pyrah noted that in greenhouse-grown plants seed set was high among chasmogamous plants. He suggested that the low seed set reported for wild plants was simply a result of the promptly disarticulating mature spikelets.

A large series of collections of a single species of *Leersia* typically shows a wide range in height from robust to depauperate. Such variation is phenotypic and probably the result of varying combinations of water level, period and depth of inundation, and concentration of nutrients in water or soil.

Nastic movements have been reported for the southeastern Asian species (Monod de Froideville). It is uncertain whether they are present in any New World species.

Leersia hexandra Sw. is a major weed, especially of rice fields, in at least 20 tropical countries in both hemispheres (Holm *et al.*). *Leersia oryzoides* is a minor weed in wet soils and rice fields in some areas of the southern United States.

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Under subfamily references see ARBER (1925, 1934); BENTHAM (1883); CLAYTON; CLAYTON & RENVOIZE; GODFREY & WOOTEN; GOULD & SHAW; HITCHCOCK; HOLM *et al.*;

⁹*Leersia nebraskensis* (J. Thomasson) G. Tucker, comb. nov., based on *Archaeoleersia nebraskensis* J. Thomasson, *Am. Jour. Bot.* 67: 877, 1980. Since the fossil species is evidently most closely related to *L. ligularis*, a species of the more advanced sect. LEERSIA, it seems appropriate to treat it as a species of *Leersia*.

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Subtribe **Zizaniinae** Honda, *Jour. Fac. Sci. Univ. Tokyo Bot.* 3: 5, 9. 1930, "Zizaniaceae."

6. **Zizania** Linnaeus, *Sp. Pl.* 2: 991. 1753; *Gen. Pl.* ed. 5. 427. 1754.

Tall, monoecious annuals [perennials] of shallow fresh or brackish waters. Rhizomes lacking [present]. Stems solitary (often producing several tillers) [densely caespitose], unbranched, erect [decumbent, rooting at the nodes]; nodes glabrous. Leaves several, cauline [mostly basal]; sheaths about as long as leaf blades, glabrous (sometimes ciliate on the margins); ligules about as high as the width of the blade; blades flat, linear-lanceolate [linear], both surfaces generally glabrous (but pilose just above sheath), margins hispid. Inflorescences terminal [or both axillary and terminal], paniculate, the staminate branches below the carpellate ones; nodes densely hirsute; branches glabrous. Spikelets 1-flowered, disarticulating below the lemmas, the carpellate lanceolate, appressed-ascending at anthesis, the staminate ellipsoid, pendulous. Glumes nearly obsolete (reduced to collarlike ridges). Lemmas broadly lanceolate to linear, staminate ones 3-nerved and carpellate ones 5-nerved, acuminate, with awns up to 3 times as long as body of the lemma. Paleas linear-lanceolate, equaling the lemmas, hyaline, 3-nerved, acute. Flowers imperfect. Stamens 6; filaments short, very slender (barely elongating, the palea and lemma spreading, exposing the dehiscent anthers); anthers linear, the apex of the connectives not prolonged. Ovaries slender, glabrous; styles short, glabrous; stigmas 2, longer than styles, aspergilliform, exerted before anthers. Caryopsis narrowly cylindrical, firmly clasped by the indurate carpellate lemma. Base chromosome number 15. LECTOTYPE SPECIES: *Z. aquatica* L.; the other Linnaean species, *Z. terrestris* L., was excluded by Bentham (*Gen. Pl.* 3: 1115. 1883). (Name from Greek *ziza-*

nion, a weed of grain fields, the tares of the New Testament parable; cf. Matthew 13: 24-30.)—WILD-RICE.

A small genus (four species) of eastern North America and eastern Asia. Three species occur in North America (Dore), two of these in the Southeast. *Zizania aquatica* L. (lemmas and paleas scabrous throughout, grains about 12 times longer than wide), northern wild-rice, $2n = 30$, occurs from New Brunswick to Manitoba, south to Florida and Texas. It consists of two varieties: var. *aquatica*, southern wild-rice, grows over the entire range of the species; var. *brevis* Fassett, estuarine wild-rice, only on freshwater tidal shores of the Saint Lawrence River in Quebec (Darbyshire & Aiken; Fassett). The second species, *Z. palustris* L. (*Z. aquatica* var. *angustifolia* Hitchc.) (lemmas and paleas hispidulous apically, otherwise glabrous, grains 6-8 times longer than wide), $2n = 30$, occurs from Nova Scotia to Manitoba (introduced in Saskatchewan), south to Maryland, Missouri, Arkansas, and Kansas. This species also consists of two varieties (Dore): var. *palustris*, northern wild-rice, occurs over the species range, while var. *interior* (Fassett) W. Dore, river wild-rice, is found from southern Ontario to Iowa. Fassett and others have treated *Z. palustris* as a variety of *Z. aquatica*. The two species differ vegetatively and ecologically, as well as in spikelet morphology. *Zizania palustris* generally has narrower leaf blades and grows in deeper water than *Z. aquatica* (Dore). Electrophoretic evidence confirms the separation of *Z. aquatica* and *Z. palustris* at the specific level (Warwick & Aiken).

The third North American species, *Zizania texana* Hitchc., Texas wild-rice, $2n = 30$, is endemic to warm springs in central Texas (Correll & Correll). Unlike *Z. aquatica* and *Z. palustris*, which are annuals, *Z. texana* is a perennial, its prostrate stems rooting at the nodes. It appears to be most closely related to *Z. aquatica*, since plants of both species have scattered prickles on the lemmas. The grains of *Z. texana* are 50-70 percent as long as the palea, while those of *Z. aquatica* are about as long as the palea. *Zizania aquatica* has erect, emergent leaves, while *Z. texana* has submersed, flexible ones. The species is considered endangered; it is known only from the type location in Hays County, Texas, where it grows in calcareous spring waters that have a year-round temperature of 21.5°C.

The fourth species, *Zizania latifolia* (Griseb.) Stapf, Manchurian wild-rice, $2n = 30, 34$, is native to eastern Asia (Korea to northern India). It is a stout, stoloniferous perennial that differs from the three North American species in having apically ciliate pedicels. The awns of the carpellate lemmas are shorter than those of the North American species. It is hardy in the vicinity of Washington, D. C., but in that climate does not flower early enough to set fruit each year. It can be grown outdoors in Ottawa, Canada, but does not flower there. Hybrids of *Z. palustris* and *Z. latifolia* are sterile (Dore).

Because of the economic importance of wild rice, its ecological requirements are well known. The best crops are harvested where there is some movement of water, as in slow rivers or in freshwater coves or bays near the mouths of streams. A stable water table during the summer is necessary; wild rice does

not grow in water deeper than one meter (Dore), nor does it grow in brackish water.

All species are protogynous, the staminate florets of an inflorescence being exerted after the stigmas (Dore), a condition that promotes outcrossing. Greenhouse experiments have shown that pollen from an inflorescence can fertilize carpellate flowers in other inflorescences of the same plant, so *Zizania palustris* is self-compatible (Dore), as is *Z. texana* (Terrell *et al.*). However, stems flowering late in the season sometimes exert stigmas as the stamens are beginning to shed pollen (e.g., *Tucker 3841*, NYS, Preston, Connecticut). This simultaneous flowering appeared to be characteristic of short stems produced by tillering; earlier stems of the same plant seemed to be strongly protogynous. If pollen is shed when stigmas are receptive, self-pollination appears unlikely because wind would probably not carry it upward to the stigmas of the same plant. Insects gather the pollen of *Z. palustris* and *Z. aquatica* but visit only the stamens and probably do not contribute significantly to pollination. Terrell & Batra reported that individuals of *Bombus vagans* Smith (Bombidae), *Dialictus imitatus* (Smith) (Halictidae), and *Toxomerus politus* (Say) (Syrphidae) visited plants of *Z. aquatica* in Maryland. In an estuarine population of *Z. aquatica* in Preston, Connecticut (*Tucker 3828*, GH, NYS, 12 August 1987), individuals of *Apis mellifera* L., *Bombus impatiens* Cresson, and *Platycheirus quadratus* Say¹⁰ visited staminate flowers only.

Germination has been extensively studied. Caryopses of *Zizania palustris* are dormant when shed and require cold treatment (at or near freezing) for three months to break dormancy. Similar treatment (105 days at 3°C) breaks dormancy in *Z. texana*. Seeds for commercial sowing are mixed with mud, stored in large containers, and frozen over the winter. The seeds of the more southern *Z. aquatica* are less tolerant of freezing than are those of *Z. palustris*. If the seeds are stored dry, their viability rapidly diminishes, reaching one percent after only seven weeks (Fyles). Unlike the buoyant, flotation-dispersed seeds or fruits of most aquatic plants, the ripe grains of wild rice sink rapidly and the awn of the lemma sticks into the mud, anchoring the germinating seedling until adventitious roots are firmly established (Bayly), an adaptation to the flowing waters in which wild rice generally grows.

Northern wild-rice, *Zizania palustris*, is economically important. Hundreds of tons of the grain are gathered each year from lakes and rivers of Wisconsin, Minnesota, western Ontario, eastern Manitoba, and northern Saskatchewan. Much of the harvesting is done by American Indians, using methods employed since pre-Columbian times (Chambliss). Some modern harvesting is accomplished in power boats with attached flails and combines to remove grains from the panicles. Traditionally, the grain is gathered from a canoe. One person propels the canoe from the bow while the other uses two sticks, one to bend the stems over the canoe, the second to strike the panicles and knock the grains loose so they fall into it. Before they are cooked, the grains are parched to

¹⁰Insects identified by Dr. Timothy L. McCabe, Curator of Entomology, New York State Museum, where voucher specimens are deposited.

loosen the lemmas and paleas, and the chaff is separated by winnowing in a light breeze. Wild rice was a staple grain for the tribes that harvested it. It is an important food for waterfowl and is often planted to attract ducks.

The grains of *Zizania latifolia* are collected and eaten during times of scarcity in China. Shoots infected by the fungus *Ustilago esculenta* Hennings become swollen and are eaten as a vegetable, "kau-sun." The species has been introduced to Indonesia for this purpose by Chinese immigrants (Monod de Froideville). Infected plants do not flower but are propagated by division of the rhizome. *Zizania palustris* is planted for forage in the Soviet Union. It is adventive in New Zealand, where it is weedy in damp pastures.

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Subtribe *Luziolinae* Terrell & H. E. Robinson, Bull. Torrey Bot. Club **101**: 243. 1974.

7. *Zizaniopsis* Döll & Ascherson ex Döll in Martius, Fl. Bras. **2**(2): 13. 1871.

Tall, monoecious perennials [annuals] of fresh or brackish marshes and stream banks. Rhizomes stout, horizontal. Stems 1 or 2 per rhizome node, stout, unbranched; nodes glabrous. Leaves several; sheaths with free margins their entire length, glabrous; ligules deltoid, a little wider than high, sparsely hirsute abaxially; blades linear, slightly auriculate at base, with numerous transverse veinlets, glabrous. Inflorescences terminal, paniculate, with the staminate spikelets borne on the proximal portions of the branches, the carpellate on the distal; nodes pilose; branches hirsute. Spikelets 1-flowered, oblong-lanceolate, disarticulating readily at base of lemma. Glumes lacking. Lemmas broadly lanceolate, acute, mucronate or aristate (the awn up to $\frac{1}{2}$ as long as lemma), 7-nerved, glabrous. Paleas lanceolate, about as long as lemmas, acute, 3-nerved, glabrous. Flowers imperfect. Stamens 6; filaments slender, very short; anthers linear, one theca usually slightly but distinctly longer than the other, connective not prolonged. Ovaries slenderly ellipsoid, obtuse, apiculate, stipitate, glossy; styles glabrous proximally, aspergilliform distally; stigmas 2, about as long as styles, aspergilliform throughout, exerted before anthers. Achene loosely clasped by persistent palea and lemma, ellipsoid, obtuse, apiculate, contracted abruptly to a slender stipe, the surface glossy. Base chromosome number 12. TYPE SPECIES: *Z. microstachya* (Nees) Döll & Ascherson ex Döll (*Zizania microstachya* Nees), the only species included by Döll. (Name from resemblance to *Zizania*.)—GIANT CUTGRASS, SOUTHERN WILD-RICE, MARSH-MILLET.

A genus of five species (Quarín) of tropical and warm-temperate regions of the New World. *Zizaniopsis* is most closely related to *Luziola*, despite its similarity in habit to *Zizania* (Terrell & Robinson). Both genera have achenes, not caryopses, and the base chromosome number 12. The genus has never been revised. Its distinction from *Luziola* is not entirely satisfactory. While most species of *Luziola* have separate staminate and carpellate inflorescences, the only species of *Luziola* sect. *CARYOCHLOA* (Trin.) Hackel has both mixed in the same inflorescence, as in *Zizaniopsis*. Further study is needed to clarify generic circumscriptions in subtribe *Luziolinae*.

The single southeastern species, *Zizaniopsis miliacea* (Michx.) Döll, giant cutgrass, water millet, southern wild-rice, $2n = 24$, occurs from eastern Maryland southward and westward along the Coastal Plain to southeastern Oklahoma and Texas, and north along the Mississippi River to western Kentucky and southeastern Missouri. It is also known from western Mexico (McVaugh). It grows in brackish and fresh-water marshes, forming monocultures that provide shelter for waterfowl but are a poor source of food. The total productivity of cutgrass stands is about 1.3 times that of similar grass-dominated vegetation types. The leaf litter is an important contribution to the detrital base of the estuarine ecosystem.

The remaining four species occur in the lowlands of South America. *Zizaniopsis Killipii* Swallen, the only annual species, is known from northwestern

Colombia; *Z. microstachya* (Nees) Döll grows in eastern Brazil; *Z. bonariensis* (Balansa & Poitrasson) Spegaz. occurs in southern Brazil, northern Argentina, and Uruguay; and *Z. villanensis* Quarín, $2n = 24$, espadaña, is endemic to northern Argentina.

Zizaniopsis miliacea is a weed in some parts of the Southeast, where it clogs irrigation ditches and canals (Tarver *et al.*). *Zizaniopsis bonariensis* is a minor weed in temperate South America (Holm *et al.*). The young rhizomes and shoots of *Z. miliacea* can be cooked and eaten as a vegetable (Fernald & Kinsey).

REFERENCES:

Under subfamily references see BENTHAM (1883); CLAYTON & RENVOIZE; FERNALD & KINSEY; GODFREY & WOOTEN; GOULD & SHAW; HOLM *et al.*; McVAUGH; TARVER *et al.*; TERRELL & ROBINSON; and WUNDERLIN.

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8. **Luziola** A. L. de Jussieu [Gen. Pl. 33. 1789] ex J. F. Gmelin, *Syst. Nat.* ed. 13, 2: 637. 1791.

Small to medium-sized, monoecious perennials of damp soils or shallow ponds and slow streams (sometimes mostly submersed). Rhizomes soft, producing 1 to several stems per node. Stems branched, slender and erect in terrestrial plants, flexuous in submersed ones; nodes when submersed bearing roots, these with chlorenchymatous cortex. Leaves many, the uppermost floating at water's surface in submersed plants; sheaths shorter than the blades, scabrous, sometimes with transverse veinlets; ligules broadly ovoid, hyaline, basally hispid; blades narrowly lanceolate, barely auriculate, adaxial surface prickly, abaxial smooth. Inflorescences terminal and axillary, small, paniculate, the staminate panicles narrow, terminal, the carpellate ones narrow at anthesis, broadening as the branches spread with maturity; branches glabrous; nodes pilose or glabrous. Spikelets 1-flowered, ovoid to oblong-lanceolate, disarticulating at base of lemma. Glumes lacking. Lemma lanceolate, membranaceous to hyaline, 7- [to 10]-nerved. Palea lance-linear, membranaceous to hyaline, weakly 3- to 7-nerved. Flowers imperfect. Stamens 6; filaments slender; anthers linear, apex of connectives not prolonged. Ovaries ellipsoid; styles glandular; stigmas 2, about as long as styles, aspergilliform, exerted before anther dehiscence. Achene ellipsoid, strongly flattened, apiculate, cuneate at base, loosely surrounded by the persistent lemma and palea. Base chromosome number 12. (*Hydrochloa* Beauv.) TYPE SPECIES: *L. peruviana* J. F. Gmelin, the only species included by Gmelin. (Name a variation of *Luzula*, a genus of Juncaceae.)

A genus of about 12 species of the warm regions of the New World. Three species of *Luziola* are known from the southeastern United States. The others

are chiefly South American, although several extend north to the West Indies and Mexico. The only widespread southeastern species is *L. fluitans* (Michx.) Terrell & H. E. Robinson (*Hydrochloa carolinensis* Beauv., *H. fluitans* Michx.), southern water-grass, which grows in ponds and backwaters of the Coastal Plain from North Carolina (Perquimans County) south to central Florida, and west to eastern Texas. Populations in the United States and eastern Mexico are var. *fluitans*, while those in the uplands of western Mexico are var. *Oconnorii* (Guzmán M.) G. Tucker,¹¹ which differs in having longer and wider leaf blades, longer spikelets, and longer anthers (Guzmán M.). The differences in dimensions suggest that it may be a tetraploid derivative of the typical variety, but no chromosomal data are available (McVaugh).

Two other species are known in the Southeast from a few collections, although both are more plentiful in the tropics. *Luziola bahiensis* (Steudel) Hitchc. (*L. alabamensis* Chapman) (spikelets oblong-lanceolate; achenes longitudinally striate), $2n = 24$, is known in the United States only from southern Alabama (Conecuh and Mobile counties) and southern Mississippi (Forrest County). *Luziola peruviana* J. F. Gmelin (spikelets ovoid; achenes smooth) is known from western Florida (*vide* Swallen, but not mentioned by Clewell) and from southern Louisiana (Plaquemines Parish).

Most species of this genus grow in damp soils, while *Luziola fluitans* is a submersed plant of ponds and slow streams. It has been placed in a separate genus, *Hydrochloa*. Terrell & Robinson thought it to be an aquatic species of *Luziola* with reduced inflorescences, and their view is accepted here. Swallen did not comment on the status of *Hydrochloa*, although Pohl & Davidse noted that *L. fluitans* is very similar to *L. fragilis* Swallen, of South America, and that *Hydrochloa* should perhaps be included in *Luziola*. Swallen's synopsis of *Luziola* is the only systematic treatment of the genus. Davidse & Pohl (1972a, 1972b) reported several range extensions. There is need for further studies combining field work with extensive herbarium investigations to provide complete descriptions of the species and to confirm the status of *Hydrochloa*.

Chromosome numbers have been reported for several species. *Luziola Pittieri* Lucas, $2n = 24$ (Davidse & Pohl, 1972a), and *L. fragilis* Swallen, $2n = 24$ (Pohl & Davidse), are diploids ($x = 12$) like *L. fluitans*. *Luziola Spruceana* Döll, $2n = 48$ (Davidse & Pohl, 1972a), is apparently tetraploid.

Arber (1928) made a detailed study of the vascularization of the inflorescences and spikelets of *Luziola Spruceana*. She noted that the carpellate florets had six diminutive filaments subtending the ovary, and that the staminate florets had a reduced gynoeceium, features overlooked by both Bentham (1883) and Hackel. The six staminal rudiments are clearly not lodicules, two of which are present in both carpellate and staminate florets. Schuster, however, did not detect such reduced gynoecea or stamens in a similar study of *L. peruviana*. Anatomical studies of other species of *Luziola* may turn up interesting details concerning the evolution of monoecy.

Luziola fluitans is economically significant in our area, especially in Florida.

¹¹*Luziola fluitans* (Michx.) Terrell & H. Robinson var. *Oconnorii* (Guzmán M.) G. Tucker, comb. nov., based on *Hydrochloa carolinensis* var. *Oconnorii* Guzmán M., *Phytologia* 48: 77. 1981, as "*oconnorii*." (Named for Peter O'Connor.)

Its seeds and leaves are a valuable food source for waterfowl. The plants may form dense, matlike populations that interfere with recreational fishing and provide breeding grounds for mosquitoes. The species is able to tolerate prolonged periods of low water ("drawdowns") and is the most difficult aquatic grass species to control with present technology (Tarver *et al.*).

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